THE RASPBERRY WILD IN BRITAIN

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ABSTRACT

Progenies of seed of raspberry (*Rubus idaeus* L.) harvested wild from 15 English, 7 Scottish, 4 Welsh, 2 German and 2 Swiss sources were studied in the field. No new genes were found. All seedlings examined were diploid ($2n = 14$), but one rosette plant failing to flower had diploid and tetraploid shoots. The frequencies of spine colour, habit, leaf colour and leaflet number varied; one family segregated spineless plants. Most plants were hairy, in contrast to earlier reports. Investigations were made on flower bud development and flowering times; five families segregated for autumn flowering. Analyses were also made on dieback, vegetative bud-break, flower bud development, annual variation in flowering-time and fruit ripening. These biometrical characters are not essentially related to geographical origin. Male plants with healthy pollen occurred in 3 families. Males are possibly more sensitive to environment than hermaphrodites; a cycle is given to illustrate how male plants are maintained in natural populations. Six families segregated non-red fruits. Ripe fruits are mostly deep purplish-red, and markedly smaller than those of cultivated varieties. Some families had large, good flavoured fruits, suggesting derivation or introgression from cultivated varieties. The frequencies with which 7 genes were segregating in the families show a Poisson distribution. Wild raspberries are remarkably homozygous, the maximum number of heterozygous genes found in a family being four. The differences between wild and cultivated raspberries are considered in relation to the origin of " Lloyd George " : wild plants usually produce many short, hairy canes, whereas cultivated varieties mostly have tall, few, subglabrous canes. The spineless character should be of use in raspberry breeding. The absence of a recognisable cline in wild British *R. idaeus* may be attributable to Great Britain representing only a relatively small area of the natural distribution.

INTRODUCTION

Although wild *Rubus idaeus* L. is described in British Floras, populations of the raspberry wild in Britain have not been studied. Bentham and Hooker (1892) stated that although generally distributed over Britain, in some localities it may have escaped from cultivation. Druce (1932) noted its occurrence throughout Britain, except for Pembrokeshire, West Cornwall and West Kent. The wild distribution can be gauged from Figure 1, which shows that it is distributed throughout Great Britain, except for the Fen areas; in Ireland its frequency decreases from the north-east to the south-west. Raspberry seeds occur regularly in inter-glacial deposits (Godwin, 1956), and it is no doubt native, at least from late-glacial time, more especially in Scotland. Raspberry seeds, in contrast to those of the blackberry, are absent from Roman deposits.

It was hoped that a study of the progenies from seeds harvested in the wild would reveal the origins of cultivated forms, and indicate whether genes from the wild could suitably be utilised by plant breeders.

MATERIAL AND METHODS

Seeds were obtained from 26 individual plants growing naturally in England, Scotland and Wales. There were also two families from Schaffhausen, Switzerland and two from the Uppener Pass, Hanover. Table 1 gives details of the source and natural habitat of the seed parents. The seeds were sown in John Innes compost and stratified during the winter of 1954-55.

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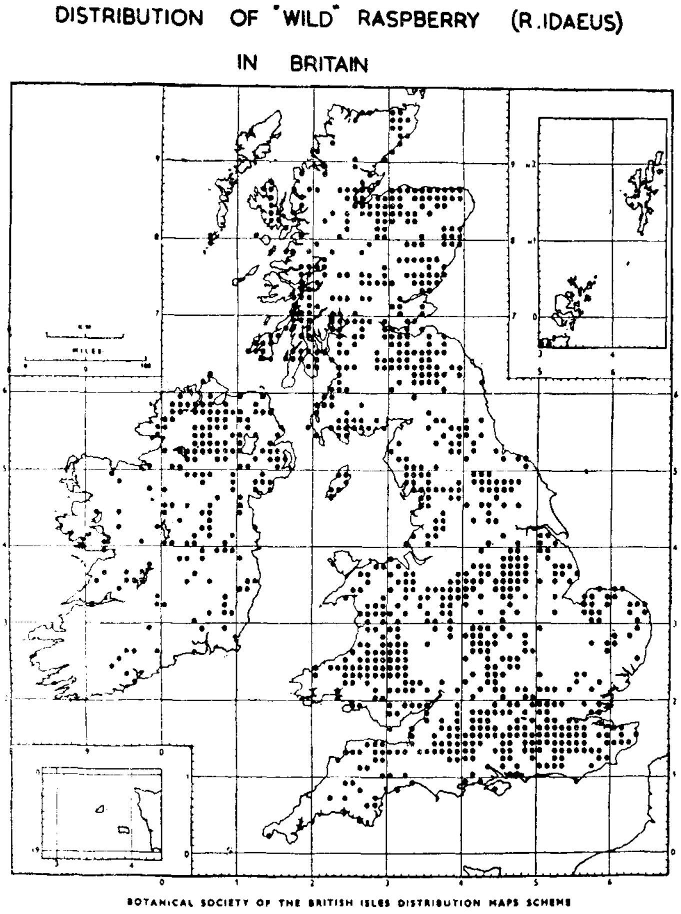

Fig. 1. Distribution map of the wild raspberry in Britain, based on records of the Distribution Maps Scheme of the Botanical Society of the British Isles. These records are not necessarily complete.

After scoring the seedlings for spine colour and intensity, and taking chromosome counts, 50 seedlings of each family were field planted in rows in June, 1955. The plants suffered badly from leather-jacket damage : the attack was at random and there was no difference between varieties in susceptibility. At an early stage the strains showed considerable variation in vigour and habit.

Several morphological characters were simply segregating, though no new morphological character simply inherited could be added to those already known in raspberry (Crane & Lawrence, 1931 ; Lewis, 1938, 1940); but there was confirmation for Lewis' (1941) belief that autumn flowering is genetically controlled. Biometrical measurements, for assessing differences in the strains, were taken during 1956 and 1957.

CYTOLOGY

Chromosome counts were made using Feulgen technique with 30 min. hydrolysis. Two or three young plants from each family were taken at random for examination. All seedlings were diploid ($2n = 14$).

One rosette type of plant was found with some atypical leaves in Fam. 30 from upper Teesdale, Yorkshire. Single crowns were separated from the rosette, and after further

TABLE 1
Sources of seed of wild Raspberries

Family No.	*Origin*	*Vice-county No.*	*Remarks*
1	East Walton Common, West Norfolk	28	Chalk. Fairly isolated
2	East Winch Common, West Norfolk	28	Peat on glacial gravel
3	Dersingham Common, West Norfolk	28	Greensand
4	Whippendell Wood, Watford, Herts.	20	
5	Yearsley Moor, Yorks.	62	*ca.* 500 ft.
6	Edge Hill, Warwicks.	38	Woodland
7	Annesley, Newark, Notts.	56	Permian limestone. Woodland
8	Coombe Hill, Wendover, Bucks.	24	
9	Great Ayton, Yorks.	62	
10	Caltan and Topcliffe, Yorks.	62	Yellow fruited parent in same locality for 40 years
11	Dalton Whin, Yorks.	62	
12	Kirkhill district, Easterness (Inverness)	96	Hillside. Clone of medium height
13	Kirkhill district, Easterness (Inverness)	96	¼ mile from Fam. 12. Plant of medium height
14	Cullen, Banff	94	Roadside. Clone of medium height
15	Cullen, Banff	94	Wood about 1 mile from Fam. 14. Dwarf clone Plenty of fruit of good flavour
16	Cullen, Banff	94	Wood. Tall plant, near Fam. 15. Good flavour
17	Cullen, Banff	94	Moor 1 mile from Fams. 14, 15 and 16. Plant dwarf
18	Glenfinnan, Westerness (Inverness)	97	Moor. Plant medium height Good flavour
(19)	Schaffhausen, Switzerland	—	
(20)	Schaffhausen, Switzerland	—	
21	Nr. Mallwyd, Merioneth	48	Roadside
22	Nr. Dolgelley, Merioneth	48	
23	Nr. Dolgelley, Merioneth	48	
24	Nr. Dolgelley, Merioneth	48	Streamside
25	Springpark Wood, nr. West Wickham, Kent	16	
26	East Tisted, Hants.	11	Edge of wood
(27)	Holzberg, Stadloldendorf, Prov. of Hanover, Germany	—	Felled forest
(28)	Uppener Pass, Hildesheim, Prov. of Hanover, Germany	—	Felled forest
29	Bishopstone Downs, Wilts.	7	Clay with flints over chalk. Scrubland on summit of downs
30	White Force, Cronkley Fell, Upper Teesdale, Yorks.	65	

growth it was seen that they fell into two classes according to leaf shape. Shoots with the more rounded and darker green leaves had tetraploid roots ($2n = 28$); those with the paler green and narrower, more pointed leaves were diploid, though such leaves occasionally occurred on the tetraploid shoots. Leaves of the tetraploid crowns had a mean stomatal size of $33{\cdot}0 \times 23{\cdot}5\ \mu$, and those of diploid crowns $21{\cdot}5 \times 15{\cdot}0\ \mu$. The clones were subjected to transmitted light from a 100 watt lamp using a blue filter, and compared with diploid and triploid cultivated varieties of raspberries. No visible differences between plants differing in chromosome number could be detected, in contrast to those Hull & Britton (1956) found in colchicine-induced internal polyploidy in *Rubus*.

Germination and Seedling Characters

The germination of seeds, sown while still in the dried fruits, was generally good. The poorest germination was in Family 10 with 25%, the highest being in Family 22 with 90%. As fruits were harvested the same year the seeds were sown, wild raspberries have a good first year germination. The mean germination for 17 families was 59% (Table 2).

Three types of seedling abnormalities were observed (Table 2). Albinos occurred in six families, pleiocotylous seedlings in eight families, and those with the first few leaves variegated in nine families. These characteristics had for all families an average frequency of ·55%, ·45% and 1·05% respectively. Family 11 produced nine albinos and nine variegated seedlings, suggesting a relationship between these two characters.

Family 5, from Yearsley Moor, had very rapid germination and produced very uniform dark green seedlings with coloured spines; Families 11 and 12 also had early germination and large seedlings. But by contrast Family 21 had small seedlings. Family 26, from Hampshire, differed from the others as its seedlings branched early and produced

Table 2

Seedling abnormalities and germination in British wild Raspberries

Family No.	*No. sown*	*No. germinated*	*No. albinos*	*No. pleiocots*	*No. variegated*	*% germination 1st year*
1	193	69	0	0	0	35·8
2	111	57	1	0	0	51·4
3	127	46	0	0	0	36·2
4	275	145	0	0	0	52·7
5	200	166	0	0	0	83·0
6	176	49	0	0	1	27·8
7	200	112	0	0	0	56·0
8	204	141	0	2	0	69·1
9	208	165	0	1	0	79·3
10	216	54	2	0	4	25·0*
11	218	154	9	0	18	70·6
12	220	118	6	0	9	53·6
13	—	203	0	3	0	—
14	230	154	0	0	0	67·0
15	—	116	0	1	0	—
16	240	187	0	0	0	77·9
17	—	306	0	0	0	—
18	—	166	0	0	1	—
19	—	47	0	1	0	—
20	—	243	3	0	1	—
21	—	61	0	0	0	—
22	280	251	0	4	0	89·6
23	240	156	0	0	5	65·0
24	—	67	0	5	0	—
25	215	148	0	1	0	68·8
26	—	182	0	0	0	—
27	—	135	0	0	0	—
28	—	154	1	0	1	—
29	—	154	0	0	2	—
	Total seedlings 4,006		% of total seedlings			
			0·55	0·45	1·05	Mean 59·3

*Very weak; all light green, yellow fruited.

leaves on short internodes. The vigour was uniform in most of the families, but the seedlings were very irregular in Family 19 from Switzerland. In Family 23 there was a yellowing of the second leaves in seven seedlings out of 60, and this also occurred in Family 29. Family 6 had small, irregular seedlings and seven out of 30 were tiny; one had white picotee edges. Mottled seedlings occurred in three families, there being five mottled in a total of 62 seedlings.

Although the families were diploid and sexual, they were highly uniform other than for spine colour and intensity. There appears to have been natural selection for a developmental balance between seedling vigour and environment leading to uniformity in the seedling population. It would be very difficult to separate these diploid, sexual populations from seedlings of constant species-hybrids of *Rubus*, or from cryptically hybrid polyploid apomicts with a high proportion of apospory.

The spine colours of seedlings (Table 3) were scored at the 5-6 leaf stage, and four grades were given (0 = green spines; 1 = tinged; 2 = pale coloured; 3 = dark coloured). Grade 0 seedlings are probably equivalent to the genetic classes *pt* and *Pt*; grade 1 to *pT* and grades 2 and 3 to *PT*. Family 10 from Yorkshire was unique in producing all green spined seedlings : the original fruit from which these were raised was yellow.

TABLE 3

Spine colour segregation. % distribution in seedlings scored at 5–6 leaf stage on 16 May 1955

		coloured			
Grade *Group*	0 *Green*	1 *Tinged*	2 *Pale*	3 *Dark*	*Unclassified*
Fam. 1	0	22·1	34·0	35·7	10·2
2	0	25·9	50·0	20·4	3·7
3	0	19·0	23·8	57·1	0
4	1·7	47·3	40·6	10·1	0
5	1·7	33·4	35·1	30·1	0
6	13·3	43·3	16·7	13·3	13·3
7	0	10·0	60·1	30·1	0
8	1·7	43·4	51·8	3·3	0
9	0	56·8	40·1	1·7	1·7
10	97·6	0	0	0	2·4
11	0	23·1	33·8	37·4	5·3
12	20·0	38·6	24·3	14·3	2·9
13	8·5	13·5	55·8	20·3	1·7
14	3·3	36·7	50·1	10·0	0
15	6·8	20·2	40·6	30·4	1·7
16	1·7	28·8	52·5	15·3	1·7
17	20·0	16·7	43·4	18·4	1·7
18	0	11·7	45·1	43·4	0
19	6·9	17·3	48·3	6·9	20·7
20	6·7	53·4	23·4	16·7	0
21	0	46·6	37·3	7·0	9·3
22	0	40·1	58·5	1·7	0
23	0	11·7	53·6	53·6	9·3
24	25·4	37·2	23·7	8·5	5·1
25	10·3	8·6	56·8	18·9	5·2
26	0	3·3	35·1	60·1	1·7
27	10·2	55·1	26·5	6·1	2·0
28	10·0	33·4	38·4	15·0	3·3
29	0	18·4	45·1	31·7	5·0

Green-spined forms are of three kinds; but all are recessive for *T*, the colour producing factor. Of the 29 families, 12 failed to segregate any green-spined seedlings, 16 segregated coloured *v.* non-coloured, and only one family (Family 10) produced no coloured seedlings. There is a ratio of 1 green to 17·31 coloured throughout the whole population, excluding Family 10, with a mean of 3 green to 51 coloured per family.

In Family 12, where seven of the 29 seedlings were devoid of spines, the lack of anthocyanin in the leaves of three seedlings indicated grade 0, and four of the seedlings showed a probable grade 1.

HABIT

The habit of the plants within each family was fairly uniform, although there were general differences between families. There was a range from straggly to upright, and dwarf to tall plants. Family 10 was a very weak, non-anthocyanic family and originated from a site where yellow raspberries had been growing for 40 years, suggesting a history of self-pollination leading to inbreeding depression during this period. Family 14 (Nr. Cullen, Banff) was somewhat vigorous, and so was Family 15 from the same source, although believed to have originated from a dwarf plant, rather suggesting that the seed parent had been cross-pollinated by a normal plant.

An outstanding feature was the heavy cane production (Fig. 2). The plants had an average of 71 canes each in their second year of growth, with a range from 31 to 127 canes per plant. Most plants had between 70 and 80 canes. At the end of their annual growing period, the canes averaged only 52 inches tall, with a range of from 39 to 72 inches. The populations of wild strains have many short, thin canes, in contrast to standard cultivated varieties. This may be advantageous for survival under natural conditions, especially in areas where dieback is severe.

The tone of green colouration of the leaves bore some relationship to seed source. The two Swiss and the two German families were distinct in having smooth, olive-green leaves, in contrast to the less smooth and lighter green leaves of British families. Family 4 (obtained locally from Watford, Herts.) had a very fine appearance, not markedly different from cultivated types. Similarly, Family 8 (Wendover, Bucks.) and Family 9

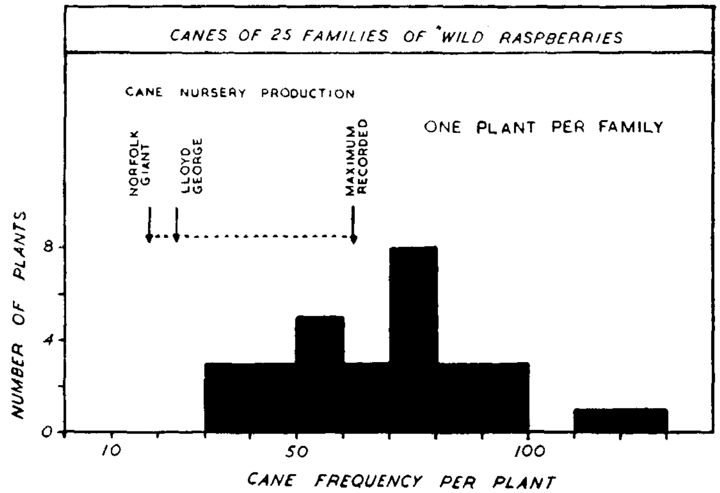

Fig. 2. Cane production in 25 British wild families. Counts are on single plants per family. The cane nursery production figures of cultivated varieties are estimates provided by Dr. C. A. Wood.

(Great Ayton, Yorkshire) had the appearance of cultivated raspberries. They had larger flowers, and fruits with a good cultivated flavour and appearance, in contrast to the smaller, darker and less pleasantly flavoured fruits of most families.

The inflorescences of the plants in Family 11 (Dalton Whin, Yorks.) lacked the deep coloration typical of the other families and of most cultivated varieties, excluding " Norfolk Giant." Their leaves were more variable than is usual for raspberries.

Leaflet-numbers on first year canes of plants within the families varied between three and five leaflets, with various intermediate grades. One family (Family 12, Inverness) was segregating plants without spines. A x^2 test for the 40 spined to 9 spineless plants for a possible 3 : 1 ratio gave $x^2 = 1{\cdot}14$, which is not significant ($P = 0{\cdot}3 - 0{\cdot}2$), and suggests it is segregating normally for this character, which results either from the parental heterozygote selfing or from sibbing with another heterozygote.

The non-prickled and prickled plants were compared in order to determine whether the lack of prickles affects vigour, as thornless wild blackberries are believed to be weaker than thorned ones. The prickled plants were 35·1 inches tall and the non-prickled were

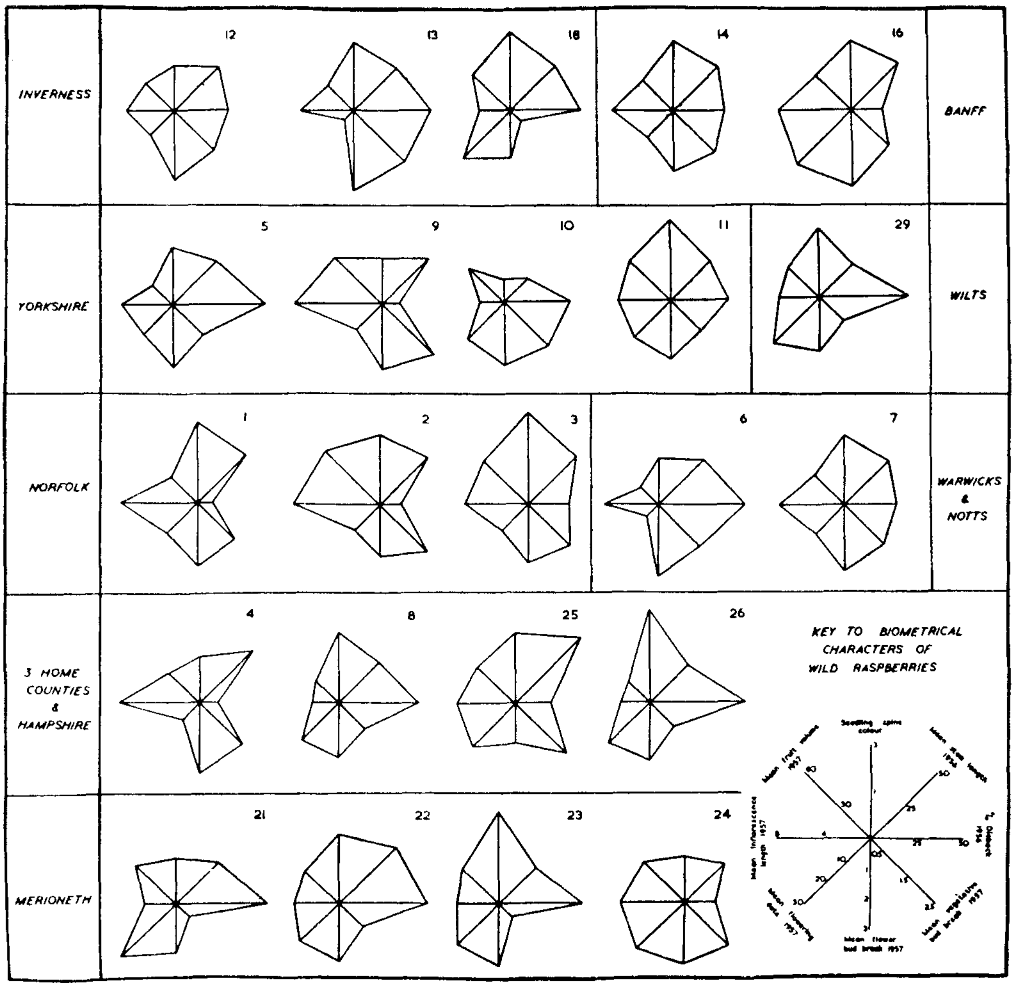

Fig. 3. Pictorial representation for eight biometrical characters in 23 British wild raspberry families, grouped according to geographical origin.

34·7 inches by 25 May, 1956; no differences in vigour are associated with the absence of prickles, The proportion of dieback in the winter of 1955-56 was 11·6% among the prickled plants, but only 4·9% among the spineless. Why these naked plants seem to over-winter with less tip-killing is not clear.

Figure 3 gives a pictorial representation of 23 of the British wild raspberry families in their mean behaviour for eight biometrical characters, with the families grouped according to their geographical origin. There is no characteristic behaviour associated with their origin, as families from the same area differ widely from each other.

HAIRY AND SUBGLABROUS STEM-TIPS

Hairiness (*H*) is most prevalent among wild raspberries (Figure 4) and only two families were subglabrous (*hh*) throughout. As classifying too early might include young plants that are first hairy but later subglabrous, scorings were made both in July and in September on two of the families (Families 1 and 13). There was a general agreement, and only four plants had to be re-classified.

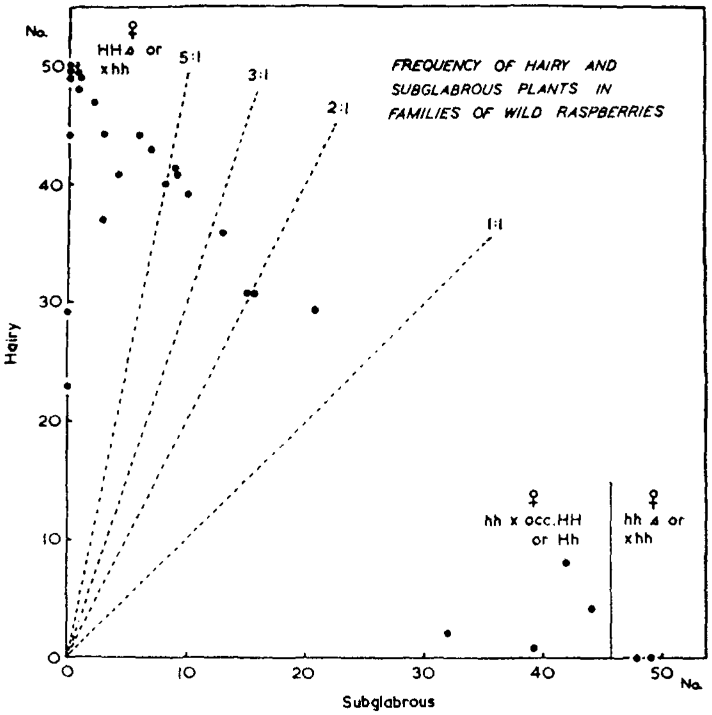

Fig. 4. Frequency of hairy plants plotted against subglabrous plants in 30 families of wild raspberries. The occasional hairy plant in an otherwise subglabrous population represents a definite cross between a subglabrous parent and a hairy pollen parent. Note the prevalence of hairy plants.

If a 3 : 1 ratio is expected from selfing or sibbing of heterozygotes (Fig. 4), then nearly all the families show a deficiency of subglabrous segregants. Grubb (1922) postulated that homozygous hairy plants do not exist in the wild; however, nine of the families were non-segregating hairy, indicating a homozygous parent. The present samplings are in contrast to the observations of Grubb who stated that in the wild the glabrous forms predominate, and that hairy plants are only found after careful search.

Four of the families were almost wholly subglabrous, with the occasional hairy plant. These must have been derived from *hh* mother plants occasionally cross-fertilised by pollen from *HH* or *Hh* plants.

FLOWERING AND POLLINATION

The developmental stages of the flowers on inflorescences were scored on 24 April, 1957 using the following key : (1) no buds showing, (2) buds clustered, (3) buds separating, (4) one flower open on an inflorescence, and (5) several flowers open. A mean statistic of flower-bud development was then calculated and the range assessed within a family, to determine whether environment has influenced this character in the history of the families. The families to show the latest flower bud development were Family 25 (West Wickham, Kent), Family 18 (Inverness), and Family 2 (West Norfolk). The earliest was Family 13 (Inverness), and this was the only family with a plant having inflorescences with several flowers open. Two other families were early : these were Family 16 (from Banff) and Family 28 (Uppener Pass, Germany).

Although the families with the earliest developing flowering buds and inflorescences were from Inverness and Banff, not all the families derived from this area are early. It is possible that a greater range of variation in this character is obtainable from this area of Scotland. This is also reflected in the mean flowering time (measured in days in June, 1956) when the families are classified by origin (Fig. 5). The Scottish families can be very early or very late. The families from the Home Counties behave likewise, but those from various parts of the Midlands, except one, are clustered together. The four families from

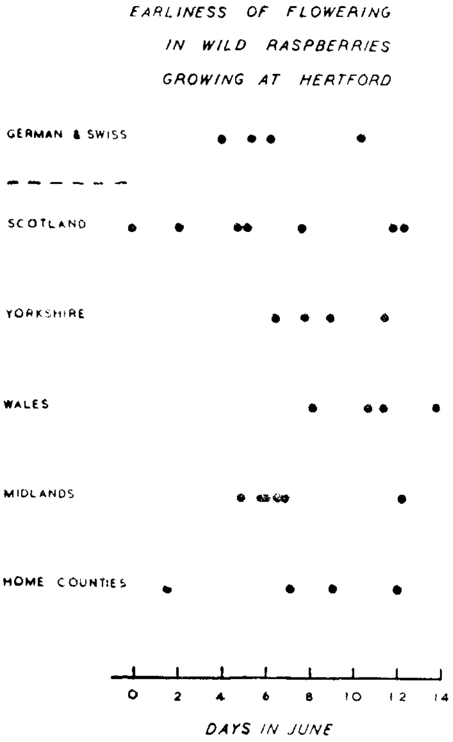

Fig. 5. Mean flowering time of 29 families growing at Hertford, grouped according to their geographical origin.

Wales and the four from Yorkshire are later and include no early families; they contrast especially with the Scottish families. Although there is a tendency within certain areas to produce families at one end of the flowering range, there is no definite association of this character with any geographical area.

Most families still had odd flowers and occasional buds showing on 26 June, 1957, even though ripe fruits were often present on the same plants : there is about two months extension of flowering period. No bees were seen working the raspberry plot on this date, although bees normally prefer raspberries to most other crops. The odd late flowers are less likely to be cross-pollinated than flowers at the height of the flowering season.

All the families were immensely attractive to hive bees, and various bumble bees. Although the bees are attracted by the prolific nectar, they also made regular attempts to work inflorescences that had expanded but whose buds had not yet opened (stage 3). Part of the attraction for bees may lie in the general shape of a raspberry inflorescence itself. By comparison, *Rubus caesius* L. growing on the same plot was rarely visited by bees, but attracted hover and other flies.

There were two plants with double flowers in each of Families 3 and 9. The two plants in Family 3 had extra petals, but in Family 9 one plant had double petals and sepals, and another triple sepals, and double petals from converted stamens. A gene for sepaloidy is known in raspberry; it was not possible, however, to determine whether this was the one with variable penetrance responsible for these sepaloid flowers.

AUTUMN FLOWERING

True autumn flowering is the occurrence of inflorescences terminally on the current year's canes. Confusion can be caused when there has been considerable dieback of second-year canes and new shoots arise from them low down. Autumn flowering is a discrete character and on the same plant either none of the current year's canes have terminal inflorescences or nearly all of them do. The symbols *Af-af* are assigned to it.

Five families were segregating for autumn flowering by the end of August. There was, however, no relationship between this character and the geographical origin of the families; for example, only one of the West Norfolk families was segregating for autumn flowering. Only one plant was autumn flowering in three of the families, but in Family 15 (Banff) there was a ratio of 40 summer only : 10 summer and autumn flowering, and in Family 18 (Inverness) there was a ratio of 42 : 8. x^2 tests for each of these two families showed there were no significant differences from an expected 3 : 1 ratio.

There was no evidence, either from the appearance of the plants, or from examination of the pollen-grains of some autumn flowering plants, that they were other than diploids. This contrasts with the observations of Lewis (1941) on cultivated varieties of autumn flowering raspberries formerly grown in England, which were always either tetraploid or (occasionally) triploid.

MALE PLANTS

Male plants are readily recognised by their foliage and by the rounded shape of their flower buds. Two genes control sex : *MF* plants are hermaphrodites and *Mf* plants are males. Three families (from West Norfolk, Inverness and Merioneth) were segregating for male plants, which indicates that this gene is widely spread in the population wild in Britain. There were 106 normals and 29 males in these three families, which is very close to, and not significantly different from, a 3 : 1 ratio.

Fig. 6 shows how the male plants are perpetuated. Although they have good powers of vegetative propagation, they are unable to reproduce directly by seed; but males segregate from either selfings or sibbings of *Ff* plants. As male plants produce much good pollen, this will permit their crossing to *FF* plants, and so continue to produce hermaphrodite heterozygotes. They will give a 1 : 1 ratio of hermaphrodites and males should they backcross to the heterozygote.

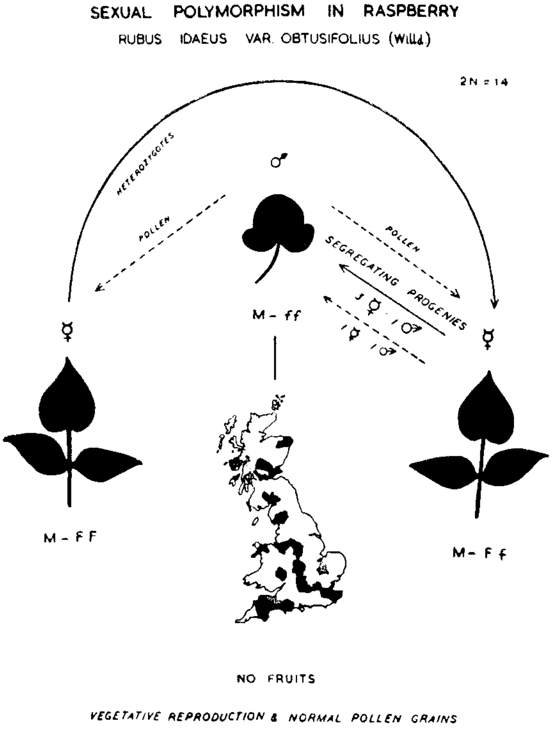

Fig. 6. The distribution of male raspberries found growing wild in Britain, and a diagram showing the pollination cycle which maintains the populations of male plants. These have fertile pollen but do not produce seeds.

Figure 6 also shows the known vice-county distribution of male plants : two doubtful records, marked in stippling, are included. Male plants have not been recorded wild in England east of the Pennines, nor until now in East Anglia. They are also absent from south-east Scotland. This suggests that plants recessive for *ff* are more sensitive, either during germination or in later growth stages, to the drier conditions of eastern Britain with its cold brisk winds.

The lengths and breadths of ten dry pollen grains were measured in eight wild families, six standard cultivated varieties and six inbred lines. The pollen-grains of the wild raspberries are the same size as those of cultivated varieties. There is a limited range of 7·5 μ in length and of 2 μ in breadth; this means that selection from the wild has not been accompanied by selection for pollen-size. Comparison in Family 3 between dry pollen-grains of hermaphrodite and male plants suggested a very slight increased size for male plants. The values for stained pollen-grains, however, were 29·8 $\pm$ 2·2 μ and 30·0 $\pm$ 2·3 μ for two hermaphrodite plants and 29·5 $\pm$ 1·6 μ and 28·5 $\pm$ 2·4 μ for two male plants; sex of the parent clearly does not influence pollen size.

FRUIT COLOUR AND SIZE

Only six families segregated for fruit colour, Table 4. Most of the red fruits were much deeper coloured, with almost a purple tone, than those of cultivated varieties, and they darkened very rapidly. In this characteristic the wild raspberries were differentiated clearly from cultivated varieties, but not all the families had " wild type " fruiting. For example, Family 2 (West Norfolk) had large, good flavoured fruits resembling those of cultivated varieties, in contrast to the small round purplish-red berries of most of the families. Such a characteristic strongly suggests that this family originated as an escape from cultivation.

TABLE 4

Fruit colour segregation. (Other families were red-fruited only)

Family No.	*No. Red*	*No. Apricot*	*No. Yellow*
7	13	0	2
13	25	2	0
15	31	1	0
17	34	2	0
24	44	4	3
25	41	0	1
	Total 188	9	6
10*	0	0	12
22†	50	0	0

*Yellow fruited parent. †Amber fruited parent.

There were 188 red : 9 apricot : 6 yellow fruits in the six segregating families (Table 4). If the parents were heterozygous for P and T, the genes controlling fruit and spine colour, then the F_2 should segregate 12 red fruited : 3 apricots : 1 yellow. Even allowing for variations in the pollination system, it appears that there is an excess of red-fruited plants; Crane and Lawrence (1931) had observed that the proportion of non-red fruits in cultivated varieties was below expectation. Only one of the families was homozygous (*pptt*) for yellow fruits; on the other hand, Family 22 (Merioneth) from an amber coloured fruit produced an all-red progeny.

The distribution of fruit size in the 25 English wild families (measured as the volume of 10 fruits of ten plants in each family) and the fruit volumes of ten cultivated varieties from an adjacent plot are shown in Fig. 7. The differences in fruit size are very marked, but are unlikely to be due to differences in growing conditions, and if the cultivated clones were virus infected this would only have reduced these differences. Only the Canadian variety " Rideau " had small fruits, and there is a fair spread in size for the cultivated varieties. In the wild families, the fruits of Family 2 (West Norfolk) not only were large, but had the good flavour and general appearance of a cultivated variety. The values for size in the various wild families tended to be more clustered together. Small fruit-size is a particular character of the wild raspberry that now separates it from the modern cultivated forms.

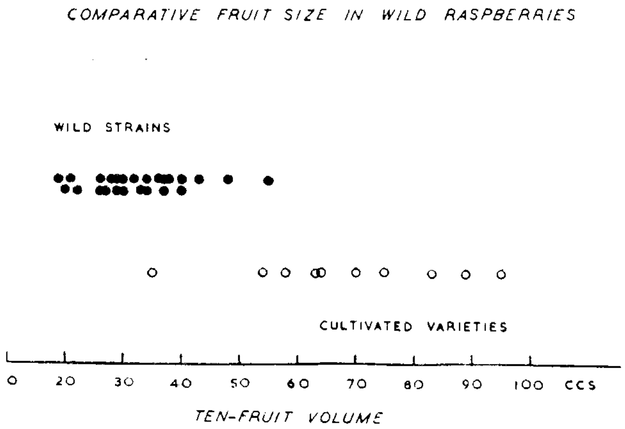

Fig. 7. Fruit sizes in the wild raspberry families compared with those of cultivated varieties growing on an adjacent plot. Fruit size is the mean volume of ten fruits for ten plants in a family, and of ten fruits in each cultivated variety.

Allelic Frequencies

Altogether eight known genes affect habit, floral and fruit characters. They were recorded in the families (Fig. 8), but there was no segregation for green *v.* pale green leaves (*G–g*). Twelve alleles are now known in *R. idaeus* but some, such as *W–w* (which affects the pollen germination) and *X–x* (hypocotyl colour in young seedlings), require special conditions for determination. The frequencies with which the seven genes were segregating

SEGREGATIONS IN 25 BRITISH "WILD" RASPBERRY FAMILIES

SYMBOL	SEGREGATING	NOT SEGREGATING		PHENOTYPE	
		DOMINANT ONLY	RECESSIVE ONLY	DOMINANT	RECESSIVE
A - a	5	20	0	SUMMER FLOWERING ON 2nd YEAR CANES	DITTO + TERMINAL AUTUMN FLOWERING ON 1st YEAR CANES
D - d	1	24	0	NORMAL FLOWERS	SEPALLOID FLOWERS
F - f	3	22	0	☿ FLOWERS (WITH 3-5 LEAFLETS)	♂ FLOWERS (WITH SINGLE LEAVES) = VAR. OBTUSIFOLIUS
G - g	0	25	0	DARK GREEN LEAVES	PALE GREEN LEAVES
H - h	17	7	1	HAIRY STEM-TIPS	SUB-GLABROUS STEM-TIPS
S - s	1	24	0	SPINED	SPINELESS
T - t	13	11	1	COLOURED SPINES	GREEN SPINES
P - p	6*	18	1	RED FRUITS - GREEN LEAVES	YELLOW FRUITS - PALER LEAVES (DUE TO LACK OF ANTHOCYANIN)
*INTERACTION OF P & T	1 SEGREGATING APRICOT AND YELLOW 4 " " ONLY 1 " YELLOW ONLY				EXTRA PETALS OCCURRED IN 3 FAMILIES

Fig. 8. Description of the alleles for the eight known genes in raspberry affecting plant habit, and floral and fruit morphology, and the occurrence of these alleles in the British wild families.

are given in Fig. 9; this shows the relation between the number of families and the number of alleles for which they are segregating.[§] There is a good fit between the observed frequencies and a Poisson distribution. Eight families segregated for only one gene and seven for two, and it is surprising, therefore, how relatively homozygous are populations of raspberry in the wild, especially as the species is sexual and diploid. It is also curious that all five genes tested by Lewis (1938), from the 12 known, were found to be linked. The maximum number of alleles found in a heterozygous condition in any one wild family was four.

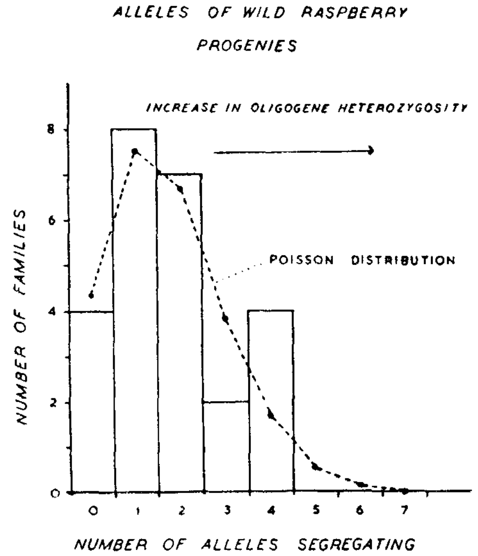

Fig. 9. The relation between the number of families and the number of alleles for which they are segregating. The theoretical Poisson distribution is also given.

Biometrical Ranges and Correlations

The percentage dieback to the total growth during the winter of 1956/57 showed that two families from West Norfolk, and from Hertfordshire and Yorkshire, had the least dieback, whereas three families from Hampshire, Hanover and Merioneth had the highest. Three of the four Merioneth families had over 45% dieback, yet the fourth had only 17%. Even within the same vice-county there may be wide differences in dieback, showing that being derived from a local environment is not a factor immediately responsible for the differences.

Vegetative bud-break, an important character in relation to frost damage early in the year, was measured as the mean bud-break index by 11 March, 1957. The earliest families were the two from Switzerland and Germany, whereas an Inverness family and two of the families from Merioneth were the latest. Yet another Inverness family (Family 13) was among those with the earliest vegetative bud-break in the British families; hence even this character shows no clear-cut association with origin.

In flower-bud development by April, 1957 (measured as the flower-bud index), one Inverness family was the earliest and the Kent family was the latest. The differences in mean inflorescence length on 28 April, 1957 ranged from that of a Yorkshire family (7·7 inches) to that of another Yorkshire family with inflorescences only two inches long. Thus there are considerable differences even between progenies from the same area.

The earliness of flowering, as measured by mean date in May, 1956, gave two early families : Family 13 (Inverness) and Family 16 (Banff) : these were also the earliest flowering in 1957. The latest families to flower in 1956 were Family 21 (Merioneth), Family 17 (Banff) and Family 29 (Wiltshire). In 1957 only one late family was the same, *viz.* that from Wiltshire. Family 18 (Inverness) and family 24 (Merioneth) were also late. Late flowering is not so distinct and regular each year as early flowering. The contrast between early and late flowering of strains from the same area such as Inverness, together with the general annual correlation, strongly indicates that although flowering time is intrinsic to a strain, it is not necessarily related to the geographical origin.

The times taken to produce ripe fruit after flowering in 1956 were fairly close for all families. Two of the Merioneth families ripened within 34 days and 38 days respectively, whereas a Banff family and a Swiss family took 44 days. Hence even time taken to ripen is not associated necessarily with the original source. The three families with the largest fruits (as 10-fruit volume) included two of the families from West Norfolk (with 54 and 48 c.c.), and one from Yorkshire (48 c.c.). The family from Warwickshire had a mean of only 19 c.c. The largest-fruited families also had the best flavour and appearance (see Table 5), and may represent introgression from cultivated varieties, or have arisen as escapes from cultivation.

TABLE 5

The possibility of escape from cultivation or introgressive hybridisation

As indicated by	*Family No.*
" Cultivated " or fine appearance	4, 8, 9, 16, 25
More vigorous growth	14, 15
Largest, good flavoured fruits	2, 9
Thicker stems of inflorescences	21

Nine families out of 25 looked like escapes from cultivation.

The possibility of correlations between the means of the biometrical characters was examined. There were no correlations between mean flowering-date with percentage dieback, nor for stem-length with dieback. Mean flowering-dates in 1956 plotted against mean fruiting-dates in July showed a positive correlation, but as the mean fruiting-date range was only between 13 and 19 July, and flowering-date only from 1 to 9 June, the clustering of the time factor masked most of the correlation (*cf.* Haskell, 1955). Mean inflorescence-length on 28 April, 1957 plotted against mean flowering-time (May, 1957) shows a negative correlation, which indicates that an early assessment of the earlier flowering families might be made : but such a correlation is only to be expected, as the earlier inflorescences would start to elongate earlier.

" WILD " AND " CULTIVATED " RASPBERRIES

The absence of triploids and even tetraploids from the chromosome counts of 80 plants does not rule out their possible occurrence. The wild American red raspberry (*R. strigosus*) is diploid (Longley & Darrow, 1924), and is akin to *R. idaeus* with which it easily inter-crosses. However, three plants of *R. strigosus*, examined by Einset (1947), were triploid ($2n = 21$). Possibly these were seedlings from diploid plants in Bailey's Botanic Garden which had hybridised with cultivated tetraploid raspberries. Vaarama

(1954) examined a wild plant of *R. strigosus* from Newfoundland, which was diploid, and commented that even Longley and Darrow's observations were on cultivars derived from this species. Actually they examined one wild plant and four horticultural varieties, finding meiosis regular in all; both the wild plant and one of the varieties had 100% good pollen.

The fertility of eight British plants, determined by the frequency of well-stained pollen grains in acetocarmine jelly, gave over 75% of good grains in all plants (Table 6). There has been no selection or correlated response for increased pollen grain size and changes in fertility during domestication of raspberry from the wild. Selection in the cultivated raspberry has mainly involved reduction in number of canes and their increased growth and vigour, as well as increases in carpel-size and larger fruits. At the same time, selection has been for those plants whose fruits remain light red after ripening, by breeders rejecting the very dark and purple-red fruiting types. The dual phenomenon of numerous and short canes of the wild types strongly suggests that the supposed truly wild ancestry of a recent cultivated variety, like " Lloyd George," is open to question. This does not, of course, rule out the more likely possibility that it is an escape growing in the wild from seeds of a cultivated variety disseminated by birds. The differences in cane and fruiting characteristics of wild (W) and cultivated (C) raspberries are given in Fig. 10.

TABLE 6
Fertility in wild and cultivated raspberries

% *Pollen grains stained*	*Number of plants*		
	Wild families	*Cultivated varieties*	*Cultivated inbred lines*
41-50	0	1	0
51-60	0	0	0
61-70	0	4	1
71-80	2	4	0
81-90	1	3	1
91-100	5	12	4

According to Markham (1936) and others, " Lloyd George " was found in a wood in Dorset by J. J. Kettle, and this origin has been widely accepted. This seems unlikely, as " Lloyd George " possesses many characters superior to those of wild plants in these experiments, *e.g.* it averages only 24 canes per plant. A search for raspberries in Dorset around Poole failed, and this made one also suspect that " Lloyd George " did not originate in Dorset. Oldham (1946) clearly states that Kettle obtained it as a chance seedling growing in a wood in *Kent*, later moving to a fruit farm at Corfe Mullen, Dorset, from where he introduced the variety in *c*. 1919. He also raised the variety " Corfe Mullen Wonder " from " Lloyd George."

These statements accord more with the evidence from my experiments. The " cultivated " characteristics of families raised from seed parents growing wild in Greater London (*e.g.* at Watford, Herts. and West Wickham, Kent) indicate that they are chance escapes of local popular varieties in cultivation, probably from seed distribution by birds. Hence it is unnecessary to attribute to " Lloyd George " an immediately " wild " ancestry, as it is most likely a segregant from a popular variety already cultivated in Kent prior to 1918. Its origin may be little different from a variety like "Norfolk Giant", believed to have appeared as a chance seedling in a Norfolk garden, *i.e.* from an already domesticated variety.

COMPARISON BETWEEN RED FRUITED BRITISH WILD AND CULTIVATED RASPBERRIES

CANES	
VIGOUR C	VIGOROUS (IF VIRUS FREE)
W	WEAK TO VIGOROUS (PROBABLY VIRUS FREE)
HEIGHT	OFTEN TALL AND FEW
	MUCH MORE NUMEROUS AND SHORTER
HABIT	ERECT, RIGID OR SLIGHTLY DROOPING REDUCED VEGETATIVE SPREAD
	ERECT, RIGID PRONOUNCED VEGETATIVE SPREAD
PUBESCENCE	MAINLY GLABROUS
	MAINLY HAIRY
COLOUR	GREEN BECOMING REDDISH
	GREEN BECOMING REDDISH-BROWN
SPINES	SMALL, INFREQUENT OR ABSENT. GENERALLY LIGHTLY PIGMENTED
	INTENSE, LARGE PRICKLES. MORE HEAVILY PIGMENTED
FOLIAGE	MEDIUM GREEN SOMETIMES WITH REDDISH COLOURATION
	SAME
FRUITING LATERALS	MEDIUM LENGTH
	RATHER SHORT, WITH SMALLER FLOWERS

FRUITS	
SIZE C	LARGE OR VERY LARGE
W	VERY SMALL OR SMALL; LARGER IN SOME FAMILIES
DRUPELETS	LARGE
	GENERALLY SMALL
TEXTURE	FIRM AT MATURITY
	CRUMBLING AND GENERALLY VERY SOFT WHEN RIPE
COLOUR	MEDIUM RED, BRIGHT, NOT DARKENING
	VERY DARK RED OR REDDISH-PURPLE
FLAVOUR	GOOD OR FAIRLY GOOD
	MOSTLY POOR (INSIPID), GOOD IN SOME FAMILIES
PICKING QUALITY	FRUITS CONSPICUOUS, EASILY PICKED
	OFTEN HIDDEN BY HEAVY CANE GROWTH FAIRLY EASILY PICKED
SEASON	EARLY TO MIDSEASON
	SIMILAR

Fig. 10. Comparison between red fruited British wild and cultivated raspberries. C — cultivated stocks; W = wild families.

There are 41 subglabrous and 12 pubescent modern varieties listed in Leemans & Nannenga (1958). The subglabrous character is either attractive to plant breeders, or is linked with characters that make a good commercial variety, for this frequency contrasts markedly with that in the British wild populations. Knight, Keep & Briggs (1958) have found genetic resistance to the virus-carrying aphid in the old variety " Baumforth A," which is subglabrous. Yet somatic mutations may occur for this gene, as the usually subglabrous "Malling Enterprise" occasionally produces a few pubescent canes. Crane & Lawrence (1931) found no homozygous hairy (*HH*) forms among cultivated varieties, and heterozygotes selfed or inter-crossed gave significantly greater proportions of subglabrous forms than expected. This was not found in those wild families segregating for the gene.

Two points emerge from the standpoint of the practical plant breeder. Firstly, no characters were segregating in these families not already known to geneticists; indeed the number of genes known in raspberry is small. Secondly, except for the spineless character, none of the genes appear to offer an improvement to those already in cultivated varieties, although male-sterile lines may have value in producing F_1 hybrids. Immediately a particular gene from the wild, such as spineless, is introduced into a cultivated stock, the associated biometrical characters such as vigour, fruit-size, and general habit would also affect the cross. A series of backcrosses would be necessary before the standard of the original cultivated stock was re-attained. Hence contemporary raspberry breeding is more likely to benefit from utilisation of the available cultivated varieties, as recently demonstrated by using " Baumforth A" to obtain aphid resistance.

Although the samples were taken wild throughout Britain, this area represents only a fraction of the northern distribution of the red raspberry. Hence it is not surprising that no clines for the biometrical characters were found. Sampling over an even wider range may show more clearly a pattern in the variation, and this viewpoint is supported by the known differences between the European red raspberry (*R. idaeus*) and North American red raspberry (*R. strigosus*). These differences, which include characters like die-back, prickle density of the upper part of mature shoots, and other minor biometrical characters, have been interpreted as indicating either that *R. strigosus* is a variety of *R. idaeus*, or that they are separate species. But, as Darrow (1920) has shown, many American cultivated varieties show a mixture of characters from both. Red raspberries are fully interfertile, and the range of variation simply represents part of the variability shown by *R. idaeus* across its northern distribution.

Further study of the variation of *R. idaeus* across its range might help to show how these differences in seemingly unimportant biometrical characters are bound up with local ecological differences. It might also help us to understand the gamut of variation which is bound up with the classification of the genus *Rubus*.

ACKNOWLEDGMENTS

The writer wishes to thank members of the Botanical Society of the British Isles for supplying most of the seeds, and the Director of the Distribution Maps Scheme for permission to use the distribution map.

REFERENCES

BENTHAM, G. & J. D. HOOKER, 1892, *Handbook of the British Flora*; London.

CRANE, M. B. & W. J. C. LAWRENCE, 1931, Inheritance of sex, colour, and hairiness in the raspberry, *Rubus idaeus* L., *J. Genet.*, **24**, 243-255.

DARROW, G. M., 1920, Are our raspberries derived from American or European species ?, *J. Hered.*, **11**, 179-184.

DRUCE, G. C., 1932, *Comital Flora of the British Isles*; Arbroath.

EINSET, J., 1947, Chromosome studies in Rubus, *Gentes Herbarum*, **7**, 181-192.

GODWIN, H., 1956, *The History of the British Flora*; Cambridge.

GRUBB, N. H., 1922, Commercial raspberries and their classification, *J. Pomol.*, **3**, 11-35.

HASKELL, G., 1955, Genic and environmental relations of flowering-time in raspberries, *Genetica*, **27**, 377-390.

HULL, J. W. & D. M. BRITTON, 1956, Early detection of induced internal polyploidy in Rubus, *Proc. Amer. Soc. hort. Sci.*, **68**, 171-177.

KNIGHT, R. L., E. KEEP & J. B. BRIGGS, 1958, Resistance in the red raspberry to Amphorophora rubi (Kalt), *Proc. 10th int. Congr. Genet.*, p. 147.

LEEMANS, J. A. and E. T. NANNENGA, 1957, *A Morphological Classification of Raspberry Varieties*, Inst. v. de Vered. van Tuinbouwgewassen; Wageningen.

LEWIS, D., 1938, Genetical studies in cultivated raspberries, 1. Inheritance and linkage, *J. Genet.*, **38**, 367-379.

——————, 1940, Genetical studies in cultivated raspberries. 2. Selective fertilization, *Genetics*, **25**, 278-286.

——————, 1941, The relationship between polyploidy and fruiting habit in the cultivated raspberry, *Proc. 7th int. Congr. Genet.*, p. 190.

LONGLEY, A. E. & G. DARROW, 1924, Cytological studies of diploid and polyploid forms in raspberries, *J. agr. Res.*, **27**, 737-748.

MARKHAM, E., 1936, *Raspberries and Kindred Fruits*; London.

OLDHAM, C. H., 1946, *The Cultivation of Berried Fruits in Great Britain*; London.

VAARAMA, A., 1954, Chromosome numbers of some species and hybrids of the Genus Rubus, *Arch. Soc. 'Vanamo,'* **8**, 192-195.